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NET-WINGED MIDGES (DIPTERA: BLEPHARICERIDAE): A FOOD RESOURCE FOR BROOK TROUT IN MONTANE STREAMS

GREGORY W. COURTNEY[1] AND RICHARD M. DUFFIELD[2]

[1]Department of Entomology, Iowa State University, Ames, Iowa 50011
[2]Department of Biology, Howard University, Washington, D.C. 20059

Abstract.—We report on the importance of net-winged midges (Diptera: Blephariceridae) in the diet of three native populations of brook trout, *Salvelinus fontinalis* (Mitchill). One population, studied mostly during 1992 and 1993, was from the Rapidan River, Shenandoah National Park, Virginia. The other populations, studied in 1993 and 1994, were from Trail Creek and North Fork Rock Creek, both subalpine streams in Medicine Bow National Forest, Snowy Mountains, Wyoming. Rapidan River samples contained 411 larvae and adults, mostly of *Blepharicera appalachiae* Hogue & Georgian, recovered from 121 trout. During the study period, there were marked shifts in the relative consumption of larvae to adult *Bl. appalachiae,* then to *Bl. similans* Johannsen. These shifts presumably reflect temporal patterns of blephariceríd activity and perhaps changes in trout predatory behavior (benthic to surface feeding). At Wyoming streams, fourth-instar larvae and adults of the net-winged midge, *Agathon elegantulus* von Röder, were recovered from 34 trout. Relative to the Rapidan population, western trout populations consumed lower numbers of blephariceríds. Because net-winged midges are moderately large flies that can be seasonally abundant in many streams, we posit that blephariceríds can be a significant component of trout diets.

Key Words.—Insecta, Diptera, Blephariceridae, Net-winged midge, Trout diet, *Blepharicera, Agathon.*

Net-winged midges (Diptera: Blephariceridae) are one of the most distinctive and specialized families of Diptera. The immature stages of these flies frequent the cascades, riffles, and waterfalls of mountain streams. Larvae show many adaptations to life on current-exposed rocks, including six ventral suckers and a cephalothorax (fused head, thorax, and first abdominal segment). Larvae are grazers, using highly modified mouthparts to feed on thin films of algae, bacteria, and other organic matter (periphyton). Pupae are dorsoventrally compressed, streamlined, and attached immovably to rocks. Adult blephariceríds superficially resemble crane flies (Tipulidae) and show a diversity of habits. The females of some species are predators of insects, including other blephariceríds; however, many net-winged midges are nectarivorous or non-feeding. In most species, adults are short-lived and rarely venture beyond the riparian zone.

The Blephariceridae contain approximately 300 described species, with representatives on most major continents. The North American fauna contains 25 described species (Hogue 1987), including the western genera *Agathon* (8 species), *Bibiocephala* (1 species) and *Philorus* (4 species), and the widespread genus *Blepharicera* (12 species). The fauna of eastern North American contains eight described *Blepharicera* (Walker 1848, Loew 1863, Johannsen 1929, Alexander 1953, Hogue 1978, Hogue & Georgian 1986) and at least seven undescribed species (GWC, unpublished data).

Net-winged midges are a significant but under-appreciated component of stream ecosystems. In streams of both western and eastern North America, densities of immature stages may approach or exceed 1000 individuals/m^2 (Johns 1996; GWC,

unpublished data), making blephariceridsone of the most abundant insects and a dominant grazer (Georgian & Wallace 1983). Densities often translate into substantive secondary production, at least seasonally (Anderson 1992).

In spite of their abundance and potential trophic value, there are surprisingly few records of blephariceridsin the diet of trout or other lotic fish (Muttkowski 1929, Tebo & Hassler 1963, Tippets & Moyle 1978). This paper partially fills this gap by reporting blephariceridsin the diet of brook trout (*Salvelinus fontinalis* (Mitchill)) in eastern and western North American streams.

Materials and Methods

Virginia Samples.—From Oct 1991 to Jun 1993, stomach-pump samples were collected from brook trout in the Rapidan River, Shenandoah National Park, Madison County. The Rapidan runs generally eastward and has a predominantly gravel bottom with occasional moderate-to-large boulders. Samples were collected between the mouth of Staunton River (38°26′ N 78°22′ W, 300 m) to above Laurel Prong (38°29′ N 78°25′ W, 760 m). The park designates this section as a brook-trout management area and maintains a "catch and release" policy for fishing.

Wyoming Samples.—Stomach-pump samples were collected from brook trout in Trail Creek (41°25′ N 106°12′ W) and North Fork Rock Creek (41°27′ N 106°13′ W). Both are subalpine streams (> 2900 m) that flow eastward from the Snowy Mountains, Medicine Bow National Forest, Carbon County. Trail Creek samples were from 6 and 9 Aug 1993, and 30 Jun, 1 and 2 Jul, and 3 Aug, 1994. Samples from North Fork Rock Creek were collected on 7 and 8 Aug, 1993.

Sample Collection.—Brook trout were caught using artificial flies at various times from morning to late afternoon. Fish shorter than 150 mm were released without sampling. All samples were obtained using a stomach pump as described by Duffield & Nelson (1993). This procedure leaves the possibility that a small portion of the stomach contents is not retrieved. During the sampling process, stomach contents were placed in a small plastic pan (15 cm × 15 cm × 2.54 cm). The sample was then transferred to a 4-dram vial and preserved in 95% EtOH. Each sample was assigned an accession number associated with a specific fish. After the stomach sample was collected, the fish was measured and released. The size of the fish, time of day, weather, stream temperature and other conditions were recorded.

Advantages of using stomach-pump samples to obtain information about trout diet are discussed elsewhere (Duffield & Nelson 1993, 1999). Because samples are readily obtained over a range of times during the day as well as any time of the year, they can provide a seasonal diet profile for a particular stream and a baseline for comparative studies. Diet profiles have been used to obtain life-history data for various species of aquatic insects (Duffield et al. 1995).

Analyses.—In the laboratory, samples were sorted and identified using a dissecting microscope. All blephariceridswere placed in separate vials of 70% EtOH and subsequently identified to species. Trout-diet data were analyzed after entry into a relational database (Paradox 3.1). Insect taxa were assigned an identification code to permit summary calculations.

Specimens.—Blephariceridspecimens were deposited in the Iowa State Insect Collection, Department of Entomology, Iowa State University. The remaining material resides in the collection at the Department of Biology, Howard Univer-

Table 1. *Blepharicera appalachiae* and *Bl. similans* specimens recovered from *Salvelinus fontinalis* stomach samples from the Rapidan River, Shenandoah National Park, Virginia (1992–1993).

Date	# of samples	II	III	IV[1]	M/F	Total
17.II.1992	1	1	—	—	—	1
21–28.III.1992	12	—	3	19	—	22
5–10.IV.1992	17	1	2	26	—	29
12–19.IV.1992	13	—	3	99	—	102
22.IV–2.V.1992	14	—	—	17	—	17
31.III–3.IV.1993	10	1	1	24	—	26
2–11.V.1993	9	—	5	48	—	53
13–16.V.1993	11	—	1	22	2/0	25
23.V.1993	15	—	2	18	23/15	58
30.V.1993	5	—	—	4 (2)	5/2	13
8.VI.1993	7	—	—	(9)	9/34	52
24.VI.1993	6	—	—	(2)	1/7 (2/1)	13
TOTAL	121	3	17	187 (13)	98 (3)	395 (16)

Legend: II–IV, larval instars 2–4; IV[1], includes exuviae; M/F, adult males/females; (), *Bl. similans.*

sity. Voucher specimens of all taxa were placed in the U.S. National Museum, Smithsonian Institution, Washington, D.C.

Results

Virginia Samples.—During the sampling period, 17,153 invertebrates were recovered from 515 brook trout. No samples were collected during July. Brook trout that were sampled ranged in length from 15 cm to 27.5 cm. Of the total number of invertebrates recovered, 3360 (19.6%) were Diptera. The percentage of Diptera in each sample varied by month and sample date. A complete analysis of the taxa present in diet samples will be reported separately.

Rapidan collections included 411 blephariceid specimens: 395 *Blepharicera appalachiae* Hogue & Georgian and 16 *Bl. similans* Johannsen (Table 1). Net-winged midges accounted for 2.4% of the total trout diet. Approximately 23% (121) of samples contained at least one blephariceid. No net-winged midges were recovered in samples from August to January. The first collections of *Bl. appalachiae* larvae were in February. All blephariceids recovered in February, March, and April were larvae. By mid-May, samples contained fourth-instar larvae and adults. *Blepharicera similans* first appeared in samples from 23 May. Subsequent samples (late May and June) contained adults of both species (Table 1). Neither pupae nor pupal exuviae were recovered.

Diptera as a percentage of the total number of recovered invertebrates increased from approximately 17% in February to 20% in April and 50% in June. During this same period, net-winged midges as a percentage of the total Diptera increased from 0.3% in February to 20.7% in April and 15% in June (Table 2).

Wyoming Samples.—Thirty-four samples from Trail Creek contained at least one *Ag. elegantulus* von Röder (Table 3). Fourth-instar larvae and exuviae were recovered from samples in June and the first week of July. August samples from Trail Creek and North Fork Rock Creek contained only adult blephariceids.

At Trail Creek, 4613 specimens were recovered from 135 trout. Diptera were the dominant food item (46.7%), followed by Ephemeroptera (30%), Plecoptera

Table 2. Monthly percentages of blephariceridsrelative to the total invertebrates and total Diptera (Rapidan River, Virginia).

Month	Number of Diptera	% Diptera of total invertebrates	Number of blephariceridsrelative	% blephariceridsrelative of total Diptera
February	374	17.6	1	0.3
March	333	17.3	22	6.6
April	759	19.8	157	20.7
May	1115	37.9	164	14.7
June	434	52.0	65	15.0
July	no	samples	collected	
August	28	10.6	0	0

(13.5%) and Trichoptera (9.8%). Data from North Fork Rock Creek are based on 1307 invertebrates from 52 trout, and for most taxa show proportions comparable to Trail Creek (Diptera, 42%, Ephemeroptera, 21.3%, Plecoptera, 16.5%, and Trichoptera, 19.3%).

As with Rapidan River data, Wyoming data show that Diptera increase as a percentage of the total number of food items recovered by month (Table 4). However, unlike at the Rapidan, the monthly totals of *Ag. elegantulus,* shown as a percentage of total Diptera per month, remained relatively constant.

Discussion

Reports of net-winged midges in the diet of trout are rare. Muttkowski (1929) recorded *Bibiocephala* adults and *Blepharicera* larvae in the stomach contents of cutthroat trout (*Oncorhynchus clarki* (Richardson)) and rainbow trout (*Oncorhynchus mykiss* (Walbaum)) from the Yellowstone River. Because *Blepharicera* is not known from the Yellowstone area, the larvae recorded by Muttkowski presumably were either *Bibiocephala* or *Ag. elegantulus.* Both occur in the area (Hogue 1987; GWC, unpublished data). Tippets & Moyle (1978) found that rainbow trout in the McCloud River, California, fed primarily on benthic organisms, including "Blephariceridae". The study was based on stomach-content analysis of fish caught on three dates between 10 Aug and 10 Sep Brown (*Salmo trutta* Linnaeus), brook, and rainbow trout from western North Carolina also fed on *Blepharicera*

Table 3. *Agathon elegantulus* recovered from *Salvelinus fontinalis* stomach samples from two subalpine streams in Medicine Bow National Forest, Wyoming.

Date	Number of samples	IV	Pupae	Adult males/females
		Trail Creek		
30.VI.1994	6	9	0	0
1.VII.1994	11	21	2	0
2.VII.1994	3	4	0	0
3.VIII.1993	1	0	0	1/1
6.VIII.1993	8	0	0	3/2
9.VIII.1993	5	0	0	3/2
		North Fork Rock Creek		
7–8.VIII.1993	13	0	0	0/14

Legend: Number of stomach samples containing blephariceridsrelative; IV, fourth-instar larvae and exuviae.

Table 4. Net-winged midges as a percentage of the total Diptera recovered per month from Trail Creek and North Fork Rock Creek, Wyoming.

Month	Number of Diptera	Diptera as a % of total invertebrates/month	Number of net-winged midges	Net-winged midges as % of total Diptera/month
		Trail Creek		
June	341	34.8	9	2.6
July	678	45.2	27	4.0
August	1133	53.1	31	2.7
		North Fork Rock Creek		
August	561	42.6	14	2.5

sp. (Tebo & Hassler 1963). For the three trout species, *Blepharicera*'s contribution to the total diet was 0.2, 0.7, and 2.2%, respectively.

Although percentages less than 5% might seem insignificant, they should be viewed in terms of their seasonal contribution to trout diets. Rapidan data indicate that from February through June, Diptera and net-winged midges become increasingly important as food items (Table 2). This was especially noticeable from April through June, when blephariceridsd comprised a large proportion (≈15–21%) of recovered Diptera. By August, blephariceridsd disappeared from diet samples, presumably because their activity period had ended. Our data demonstrate that, although blephariceridsd comprise a relatively small proportion of the annual diet (2.4% of all invertebrates recovered), these flies can be an important trout food at certain times of the year.

Rapidan data provide antecdotal information about the life histories of Appalachian net-winged midges and confirm phenological predictions from other studies. Both blephariceridsd species in the Rapidan are widespread in the Applachians and demonstrate distinct patterns of larval-adult activity. Other phenological studies (Johns 1996; GWC, unpublished data) indicate that the southern- and central Appalachian species *Bl. appalachiae* typically is a late-spring or early-summer species and that the widespread *Bl. similans* is a summer species. Although these species sometimes overlap temporally in the southern Appalachians, they overlap only slightly in northern areas, including Shenandoah National Park (GWC, unpublished data). Typically, the extent of temporal overlap is that *Bl. similans* eggs are hatching (i.e., early-instar larvae are present) when *Bl. appalachiae* adults have nearly completed their emergence period (i.e., adults and mature pupae are present). Rapidan data confirm these observations. Second-instar larvae of *Bl. appalachiae* first appeared in February, second- and third-instar larvae were present in March and April, third- and fourth-instar larvae dominated early- and mid-May samples, and late-May samples included only fourth-instar larvae and adults. Only adult *Bl. appalachiae* were collected in June, which coincided with the first appearance of *Bl. similans*. Early-instar larvae of *Bl. similans* were not recorded in our samples, perhaps because the species is relatively smaller than *Bl. appalachiae* and might have been less preferred or less easily consumed by the trout we sampled. Although no samples were collected in July, we assume that adult blephariceridsd, particularly *Bl. similans,* contribute to trout diets during this month.

At Trail Creek, Diptera as a percentage of the total number of recovered items

Table 5. Emergence data for net-winged midges, Diptera and all aquatic insects from Oregon Cascade Range streams in 1982–1983 (from Anderson (1992), Anderson and Courtney (unpublished)).

Taxon	Density	% of total insects (% of Diptera)	Weight	% of total insects (% of Diptera)
		Mack Creek		
Blephariceridae	16	0.28 (0.35)	85.1	5.2 (20.2)
Diptera	4525	77.8	421	25.4
Total insects	5814		1654	
		Quartz Creek		
Blephariceridae	4	0.08 (0.10)	22.9	1.5 (4.7)
Diptera	4133	81.0	485	31.8
Total insects	5099		1525	
		Grasshopper Creek		
Blephariceridae	12	0.34 (0.48)	43	2.6 (8.6)
Diptera	2488	70.8	502	30.5
Total insects	3516		1646	

Legend: Density = number of individuals/m^2/yr; Weight = mg/m^2yr.

increased gradually over the summer from 35% in June to 53% in August (Table 4), but the percentage represented by net-winged midges remained relatively constant (between 2.6 and 4%). Comparable data were recorded in August for North Fork Rock Creek (43% Diptera, 2.5% of this being net-winged midges). This constancy of proportions for net-winged midges is markedly different from our Rapidan samples, which showed *Blepharicera* spp. increase from < 1% of all Diptera in February to nearly 21% and 15% in April and June, respectively. These data could reflect differences in the relative densities of *Ag. elegantulus* in western streams and *Blepharicera* spp. in the Rapidan River. The immature stages of *Ag. elegantulus* rarely occur in densities greater than a few hundred individuals/m^2, whereas those of *Blepharicera* spp. often exceed 1000 individuals/m^2 (GWC, unpublished data).

Another important consideration is the relative size of *Ag. elegantulus* to *Blepharicera* spp., and of blephariceridsto other Diptera. Because *Ag. elegantulus* is larger than *Blepharicera* spp., each individual represents a larger amount of energy. Therefore, use of numbers of individuals, rather than biomass, could be somewhat misleading. Blephariceridsalso are substantially larger than the dipterans that often dominate trout stomach samples (e.g., chironomids), so a blephariceridcould represent a larger source of energy than does a typical dipteran. Although we consider the Rapidan percentages (e.g., 21% and 15% of all Diptera in April and June samples, respectively) a substantial contribution to brook-trout diets, we predict that, had these data been gathered as biomass rather than as number of individuals, the relative importance of blephariceridswould be more pronounced. A 1982–83 study of three Oregon streams (Anderson 1992) confirms the relative importance of blephariceridnumbers vs. biomass. In Anderson's study, the annual productivity of blephariceridsif measured in density, was < 0.5%, a seemingly insignificant contribution; however, if measured in biomass, net-winged midges ranked substantially higher (Table 5). In fact, at Mack Creek, an ancient (old-growth) forest site, *Agathon* ranked 5th among all aquatic insects in annual biomass production (Anderson 1992; table 2). Anderson's values represent only

Ag. comstocki (Kellogg), a species not particularly abundant at any of the study sites and that typically occurs in lower densities than many western blephariceridS (GWC, unpublished data). Furthermore, in the 1982–83 study, nearly all Mack Creek *Ag. comstocki* emerged during a 1-month period (GWC, unpublished data). If data are viewed on a seasonal basis, the trophic significance of these flies becomes even greater. The same is probably true of the related species *Ag. elegantulus*. This net-winged midge is widespread in western North America, especially in streams of the intermountain west. Lowland populations are active during late spring and early summer, whereas subalpine populations are active mostly during mid- to late summer (GWC, unpublished data). During its activity period, *Ag. elegantulus* can be one of the largest and most prominent aquatic insects, and, although not usually present in high densities, it is probably an important food resource for fish.

The ecological significance of net-winged midges has been under-appreciated, yet studies have shown that densities of immature stages can exceed 1000 individuals/m^2. Even when densities are much lower, these presumably rare flies can contribute substantially to annual (biomass) stream productivity. Thus, net-winged midges are a potentially important food resource for resident fish. Our investigation has confirmed that blephariceridS contribute to trout diets and that this contribution is at least seasonally important in some Appalachian and western streams. We predict that studies of other streams will corroborate our findings and confirm the trophic significance of these unusual insects in many lotic ecosystems.

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